

Polymorphic color vision in white-faced capuchins (*Cebus capucinus*): Is there foraging niche divergence among phenotypes?

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Abstract Many species of platyrrhine primates are characterised by sex-linked color vision polymorphism. This presents an opportunity to study the biology and ecology of individuals with different phenotypes living in the same group. Several evolutionary processes could maintain polymorphic genes in populations. In this study, we evaluate the hypothesis that foraging niche divergence among monkeys explains the presence of multiple color vision phenotypes. Specifically, we test whether dichromats and trichromats differ in foraging time devoted to cryptic vs brightly colored resources. We did not find any differences in foraging time spent on different food types by dichromatic and trichromatic monkeys in two groups of white-faced capuchins (*Cebus capucinus*) living in a tropical dry forest. We conclude that in so far as these variables are concerned, niche divergence does not likely explain color vision polymorphism in our study population.

Keywords Color vision · Polymorphism · Capuchin · Niche Divergence

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Introduction

Understanding variation is a central goal in biological research. Polymorphic genes maintained in populations over long periods of evolutionary time are an interesting example of how variation can persist in nature. Of considerable recent interest is the X-linked polymorphic opsin gene present in many species of neotropical monkeys (reviewed in Buchanan-Smith 2005). Investigations into this unique occurrence of multiple color vision phenotypes will assist in the larger endeavour of identifying and understanding general processes that maintain polymorphisms in wild populations. Our project contributes to this endeavour by examining whether white-faced capuchin monkeys (*Cebus capucinus*) forage for different food resources as a consequence of their color vision phenotype.

Platyrrhine color vision

Most genera of neotropical monkeys (Infraorder: Platyrrhini) possess a polymorphic X-linked opsin gene that encodes for middle-to-long wavelength sensitive (M/LWS) photopigments. Like other mammals, these monkeys also have an autosomal opsin gene that encodes for a short wavelength sensitive photopigment. Together, this combination enables allelic trichromacy in most species of neotropical primates. Due to the sex-linked nature of this polymorphism, only heterozygous females have trichromatic vision, whereas males and homozygous females are dichromats. Frequently, three alleles with six corresponding phenotypes (three dichromatic and three trichromatic) are present in populations (Boissinot et al. 1998). The two notable exceptions to this pattern are owl monkeys, genus *Aotus* (Jacobs et al. 1993) and howler monkeys, genus *Alouatta* (Jacobs et al. 1996), which possess monochromacy and routine trichro-

macy, respectively. The X-linked opsin gene polymorphism has been retained in primate populations for up to 14,000,000 years, suggesting an adaptive function (SurrIDGE and Mundy 2002). Researchers believe the polymorphism is maintained by balancing selection (SurrIDGE et al. 2003; Yamashita et al. 2005); however, the underlying evolutionary mechanism currently remains uncertain.

Evolution and polymorphic genes

Visual specialization is an important component of the origin and adaptive radiation of primates as an order (Cartmill 2002). Selection for trichromatic vision likely followed the evolution of high-acuity spatial vision (Blessing et al. 2004). Trichromatic color vision has long been suggested as an adaptation for improved foraging efficiency (Osorio and Vorobyev 1996; Lucas et al. 1998; Caine and Mundy 2000; Sumner and Mollon 2000a; Dominy and Lucas 2001; Smith et al. 2003) but may also be important for detecting conspecifics (Sumner and Mollon 2003; Changizi et al. 2006) or predators (Caine 2002). Furthermore, in the case of neotropical primates, a satisfactory explanation for the evolutionary mechanism maintaining polymorphic color vision remains wanting. Several processes have been suggested of which four will be briefly described here: heterozygote advantage, frequency-dependent selection, mutual benefit of association and niche divergence. These were first suggested by Mollon et al. (1984) and are a subset of the many potential evolutionary processes that maintain phenotypic variation (see Hartl and Clark 1997 and Roff 2005 for a more detailed review).

Heterozygote advantage, also known as heterosis or overdominance selection, maintains polymorphisms when heterozygous individuals have higher fitness than any of the homozygotes. Trichromatic females are predicted to have higher fitness than dichromatic individuals. Of the four suggested evolutionary mechanisms, currently the most support has been mustered for this hypothesis. Trichromat advantage has been suggested for detecting or selecting ripe fruit (Osorio and Vorobyev 1996; Caine and Mundy 2000; Sumner and Mollon 2000a; Smith et al. 2003; Osorio et al. 2004; Riba-Hernandez et al. 2005) or young leaves (Lucas et al. 1998) amidst mature foliage. Alternatively, trichromatic vision may be disadvantageous under some circumstances. For instance, dichromats are better able to break camouflage than are trichromats (Morgan et al. 1992; Saito et al. 2005b), which may have associated foraging advantages. Dichromats may have an advantage for foraging on cryptic fruits (Caine et al. 2003), such as those of some figs and palms (Dominy et al. 2003), or an advantage in finding camouflaged insects (Melin et al. 2007).

While evidence of foraging situations favouring dichromatic phenotypes remains scanty, several researchers

(Mollon et al. 1984; Jacobs 1997; Smith et al. 2005) suggest dichromat advantage may potentially contribute to the maintenance of polymorphic color vision. In contrast to the heterozygote advantage hypothesis, the remaining three hypotheses assume that individuals with different color vision phenotypes are differentially suited for overcoming fitness-related challenges.

Frequency-dependent balancing selection on phenotypes operates when the fitness of any given phenotype is dependent on the frequency of that phenotype in the population (Hartl and Clark 1997). Under these conditions, uncommon phenotypes can experience strong, positive selection pressure. For example, negative frequency-dependent selection maintains different color morphs in some insect (Punzalan et al. 2005) and guppy populations (Olendorf et al. 2006), where individuals with less common phenotypes experience less predation pressure. Relevant to the current study, the frequency-dependence is suggested to be linked to the foraging abilities of the predator. This hypothesis is often suggested as the most likely, or only, alternative to heterozygote advantage (Regan et al. 2001; SurrIDGE et al. 2003; Osorio et al. 2004; SurrIDGE et al. 2005; Araújo et al. 2006). However, no evidence has yet been presented to show a relationship between the commonness of a phenotype and its relative foraging success.

The mutual benefit of association hypothesis, which has also been referred to as group selection (Mollon et al. 1984), predicts that the advantages of polymorphic color vision lie in having individuals of multiple phenotypes within a group (Mollon et al. 1984; Tovee et al. 1992). Individuals in polymorphic groups are predicted to have higher fitness than individuals in groups with low phenotype diversity. This hypothesis remains to be systematically evaluated.

Finally, the niche divergence hypothesis (environment heterogeneity hypothesis) predicts that individuals with different phenotypes will differentially exploit niches within their habitat (Mollon et al. 1984). This requires that the environment is sufficiently heterogeneous, whether in time or space, and that individuals occupy the niches to which their phenotype is best suited. Multiple alleles in populations are thereby maintained via the reduction in intraspecific competition for resources, which in turn increases the mean individual fitness. For example, Snorrason et al. (1994) found that diversification and niche specialization lead to different phenotypic morphs of arctic char, which had different diets and occupied different areas of their habitat. Polymorphic monkeys have been hypothesised to occupy different visual (SurrIDGE et al. 2003; Pessoa et al. 2005; SurrIDGE et al. 2005; Yamashita et al. 2005) or ecological (Jacobs 1998; Caine 2002; Riba-Hernandez et al. 2004) niches, or a combination thereof (Jacobs 1994; Regan et al. 2001; Osorio et al. 2004; Araújo et al. 2006) based on their

type of color vision. This final hypothesis is the subject of our current study.

It is important to note that distinctions among these hypothesised mechanisms are not always made, nor even possible. Discussion concerning them in the literature can be confusing and inconsistent. Some researchers describe four separate mechanisms, as listed above, while others lump them together. In particular, predictions of the niche divergence and frequency-dependent selection hypothesis often overlap. Because these mechanisms are not mutually exclusive and predictions are overlapping, teasing them apart remains difficult. As a starting point it is crucial to elucidate differences among individuals of different phenotypes. For example, if dichromatic advantages are found in nature, or if there is evidence of niche separation among phenotypes, then it is reasonable to believe that heterozygote advantage is not the sole (or even principle) mechanism maintaining the polymorphism and from there we could continue to evaluate other processes. Our current study contributes to this goal.

Research questions

In this study, we evaluate a major aspect of potential niche divergence by examining the foraging time budgets of dichromatic and trichromatic white-faced capuchin monkeys inhabiting a tropical dry forest in North-western Costa Rica. In our previous research (Melin et al. 2007), we established that dichromatic monkeys were more efficient in foraging for surface-dwelling insects, i.e., they captured more insects per unit time than trichromats did. We then became interested in whether or not dichromats devote more of their foraging time to finding and consuming these insects and other cryptic resources, and conversely, if trichromats spend more time foraging on foods for which they are better suited for detecting or selecting, such as red, orange and yellow fruit. Our specific research questions were: (1) Do trichromatic and dichromatic monkeys differ in time spent foraging on fruit vs insects? (2) Do trichromatic and dichromatic monkeys differ in time spent foraging on cryptic vs conspicuous fruits? (3) Do trichromatic and dichromatic monkeys differ in time spent foraging on insects that use camouflage for defense vs insects that imbed themselves in substrates for defense? We assume that dichromatic monkeys are better at tasks that require breaking camouflage, such as foraging for cryptic insects and fruit, and that trichromats are better at tasks using color signals, such as foraging for conspicuous fruit. Therefore, we evaluate three alternate predictions: (1) Individuals of a given phenotype devote more time to tasks for which they are better suited to maximise energy gain from this resource; (2) Individuals devote less time to tasks for which they are better suited because they are more

efficient at these tasks and consequently devote more time to tasks for which they are less efficient; (3) There is no ecological niche divergence in foraging time allocation between dichromats and trichromats.

Materials and methods

Study site

We conducted our study in Santa Rosa National Park (SRNP), Costa Rica. The park is located in the northwest corner of the country and is part of the larger *Area de Conservacion Guanacaste* (10°45' to 11°00' N and 85°30' to 85° 45' W). The dominant habitat is tropical dry forest and most of the trees are deciduous. The forest is highly seasonal for precipitation; the wet season begins mid-May and ends mid-December, at which point precipitation ceases almost completely until the following May.

Study subjects

White-faced capuchins, like other member of the genus *Cebus* are small, omnivorous monkeys. They live in multi-male, multi-female groups of approximately 15 individuals (Fedigan and Jack 2001). White-faced capuchins range from north-western Ecuador through Honduras and are well known for their broad diet and complex food extracting and processing behaviours (Fragaszy et al. 2004). Previous research at this site indicates that, on average, capuchins spend about half of their diurnal activity budget involved in feeding and other foraging behaviours (McCabe 2005). Their diet in SRNP is composed of 50–65% fruit and flowers, and 25–40% invertebrates (Young 2005; Melin unpublished data).

Like most neotropical monkeys, capuchins possess polymorphic color vision. This has been determined in previous behavioural (Gomes et al. 2002; Saito et al. 2005a), genetic (Shyue et al. 1998), and electroretinogram flicker photometry (Jacobs and Deegan 2003) studies. We determined the genotypes of our subjects by non-invasive fecal sample collection, PCR-based DNA typing and opsin-photopigment reconstitution. We detected all three M/LWS alleles previously reported for this genus in our population (Hiramatsu et al. 2005). To minimise the chance of mistakenly classifying a heterozygote female as a homozygote due to allelic dropout, when a female was typed as homozygous by two different samples, we required at least one sample to contain no less than 200 pg of genomic DNA in the PCR by following Morin et al. (2001). To minimise observer bias, the genotyping results were not revealed to the researchers collecting behavioural data until after observations were concluded.

We observed two habituated study groups, Cerco de Piedro (CP) and Los Valles (LV); the monkeys were individually recognizable based on a combination of age, sex, facial and body markings and scars. We observed and genotyped 17 individuals in CP and 16 individuals in LV. In the past, we have used the following age categories: Infants, <1 year; small immatures, 1–2 years; large immatures, 3–5 years; sub-adult males, 6–9 years (no sub-adult female stage); adult females, >6 years of age; adult males, >10 years of age (Fedigan and Jack 2001). However, to decrease the number of variables, we include both sub-adults and adults into one “adult” category, and small and large immatures in one “juvenile” category. Infants are omitted from analyses. Dominance rank was assigned based on the outcomes of aggressive and submissive social interactions. Only individuals more than 6 years old are included in the rank assessment. Furthermore, we only

include the two most dominant and least dominant females from each social group, CP and LV (see data analysis for details). Age, sex, social group, dominance rank and color vision typing for each individual are presented in Table 1.

Classifying food resources

Fruits

We classify fruits as “conspicuous,” “cryptic” or “other” based on the color of the mature fruits as they appeared to a trichromatic human observer. Conspicuous fruits are various shades of red, yellow or orange when ripe, which makes them highly visible to frugivores with good color vision, for example many birds, reptiles and trichromatic monkeys. Cryptic fruits are shades of green and brown and do not change color when ripe. Thus, they are relatively

Table 1 Details of individual white-faced capuchins in the study: Monkey ID, social group, sex, age, dominance rank and color vision

Monkey ID	Social Group	Sex	Age Class	Rank Group	Color Vision
Monkey 01	CP	Female	Adult		Dichromat (560/560)
Monkey 02	CP	Female	Adult	1	Dichromat (560/560)
Monkey 04	CP	Female	Juvenile		Dichromat (560/560)
Monkey 05	CP	Female	Juvenile		Dichromat (560/560)
Monkey 06	CP	Female	Juvenile		Dichromat (560/560)
Monkey 07	CP	Female	Juvenile		Dichromat (560/560)
Monkey 08	CP	Female	Juvenile		Dichromat (560/560)
Monkey 09	CP	Female	Juvenile		Dichromat (560/560)
Monkey 10	CP	Female	Adult	2	Dichromat (560/560)
Monkey 11	CP	Female	Adult	2	Dichromat (560/560)
Monkey 12	CP	Female	Adult	1	Dichromat (560/560)
Monkey 13	CP	Male	Adult		Dichromat (560)
Monkey 14	CP	Male	Juvenile		Dichromat (560)
Monkey 15	CP	Male	Juvenile		Dichromat (560)
Monkey 16	CP	Male	Adult		Dichromat (560)
Monkey 17	CP	Male	Adult		Dichromat (530)
Monkey 18	LV	Female	Juvenile		Dichromat (545/545)
Monkey 19	LV	Female	Adult	1	Trichromat (545/560)
Monkey 20	LV	Female	Adult	2	Trichromat (545/560)
Monkey 21	LV	Female	Adult	1	Trichromat (530/560)
Monkey 22	LV	Female	Adult		Trichromat (530/545)
Monkey 23	LV	Female	Adult	2	Trichromat (530/545)
Monkey 24	LV	Female	Adult		Trichromat (545/560)
Monkey 25	LV	Female	Juvenile		Trichromat (530/545)
Monkey 26	LV	Male	Adult		Dichromat (560)
Monkey 27	LV	Male	Adult		Dichromat (560)
Monkey 28	LV	Male	Adult		Dichromat (560)
Monkey 29	LV	Male	Adult		Dichromat (560)
Monkey 30	LV	Male	Adult		Dichromat (560)
Monkey 31	LV	Male	Juvenile		Dichromat (560)
Monkey 32	LV	Male	Juvenile		Dichromat (530)
Monkey 33	LV	Male	Juvenile		Dichromat (545)
Monkey 35	CP	Female	Juvenile		Dichromat (560)

Monkey ID numbers directly correspond with previous publications on this group (Melin et al. 2007)

Values in parentheses correspond to lambda max of each MLWS opsin gene (females have two, males have one)

inconspicuous to consumers in both their location amidst the foliage and in their ripeness. Our methodology for these classifications generally follows Dominy et al. (2003) and Vogel et al. (2007). A list of the fruit species included in our analyses and their classification is provided in Table 2. We placed fruits that were black or dark purple in an “other” category. We excluded these from our current analyses because dark fruits are likely to be detected on the basis of luster rather than chromaticity (Osorio et al. 2004) and because trichromats are not predicted to have an advantage detecting these colors. Thus, fruits classified as “other” should be equally conspicuous to dichromats and trichromats.

Invertebrates

We divided the invertebrates eaten by the capuchins into two broad categories, surface-dwelling and imbedded.

Table 2 Conspicuous and cryptic fruit species and corresponding families eaten by white-faced capuchins in Santa Rosa National Park

Species	Family	Classification
<i>Acacia collinsii</i>	Fabaceae	Conspicuous
<i>Acrocomia vinifera</i>	Arecaceae	Cryptic
<i>Alibertia edulis</i>	Rubiaceae	Conspicuous
<i>Bromelia pinguin</i>	Bromeliaceae	Conspicuous
<i>Bursera simaruba</i>	Burseraceae	Cryptic
<i>Byrsonima crassifolia</i>	Malpighiaceae	Conspicuous
<i>Capparis indica</i>	Capparidaceae	Conspicuous
<i>Casearia arguta</i>	Flacourtiaceae	Conspicuous
<i>Curatella americana</i>	Dilleniaceae	Conspicuous
<i>Diospyros salicifolia</i>	Ebenaceae	Conspicuous
<i>Dipterodendron costaricensis</i>	Sapindaceae	Conspicuous
<i>Ficus cotinifolia</i>	Moraceae	Conspicuous
<i>Ficus goldmanii</i>	Moraceae	Cryptic
<i>Ficus hondurensis</i>	Moraceae	Conspicuous
<i>Ficus morazaniana</i>	Moraceae	Cryptic
<i>Ficus ovalis</i>	Moraceae	Conspicuous
<i>Genipa americana</i>	Rubiaceae	Cryptic
<i>Hylocereus costaricensis</i>	Cactaceae	Cryptic
<i>Jacquinia pungens</i>	Theophrastaceae	Conspicuous
<i>Malvaviscus arboreus</i>	Malvaceae	Conspicuous
<i>Manilkara chicle</i>	Sapotaceae	Cryptic
<i>Muntingia calabura</i>	Tiliaceae	Conspicuous
<i>Psidium guajaba</i>	Myrtaceae	Conspicuous
<i>Randia monantha</i>	Rubiaceae	Conspicuous
<i>Randia thurberi</i>	Rubiaceae	Cryptic
<i>Sebastiania pavoniana</i>	Euphorbiaceae	Cryptic
<i>Simaruba glauca</i>	Simaroubaceae	Conspicuous
<i>Slonea ternifolia</i>	Elaeocarpaceae	Conspicuous
<i>Solanum hazenii</i>	Solanaceae	Cryptic
<i>Spondias mombin</i>	Anacardiaceae	Conspicuous
<i>Spondias purpurea</i>	Anacardiaceae	Conspicuous
<i>Stemmadenia obovata</i>	Apocynaceae	Conspicuous
<i>Trichilia martinana</i>	Meliaceae	Conspicuous
<i>Zuelania guidonia</i>	Flacourtiaceae	Conspicuous

Capuchins captured surface-dwelling insects by gleaning them from the surface of leaves, bark, branches and leaf litter via visual predation. We recorded the type of substrate from which the invertebrate was gleaned and, whenever possible, we identified the insect, using its common name and order and noted its color. Palatable surface-dwelling invertebrates generally use crypsis as a primary defense mechanism against predation. There are many examples of adaptations by which they accomplish this, for example, many insects have good color vision and can select the habitats which afford them the best camouflage protection, which may change over the life-cycle of the insect or the plant (reviewed in Lev-Yadun et al. 2004).

To the eye of a trichromatic human observer, most of the surface-dwelling insects caught by the capuchins in our study were camouflaged against their background substrate. We rarely observed captures of non-camouflaged invertebrates (5 out of 599 identified captures). Most often these were invertebrates found away from their usual substrate. For example, we observed a green caterpillar, which can usually be found on a leaf, to be gleaned from the bark of a brown tree trunk. Foraging time on these few non-camouflaged invertebrates was excluded from our analyses. In general, the capuchins avoided insects with aposematic coloration (Melin, personal observation). Because the vast majority of identified surface-dwelling invertebrates captured by capuchins were camouflaged, unidentified surface-dwelling invertebrates were also included in the camouflaged category for our analysis.

Imbedded (subterranean) insects include small, colonial insects, mostly hymenoptera, that dwell within substrates, such as holes, mounds or under bark, as a primary defense against predation. Capuchins acquire these invertebrates by licking them from the insides of branches, acacia thorns or nests/mounds (wasps, termites) or extracting larger insects, such as cockroaches, from under sections of bark, within branches, tree holes and crevices (Young 2005). We considered imbedded insects to be non-cryptic because they are not camouflaged and are not often detected visually. Instead, olfactory and auditory senses, as well as previous experience in finding them, are more important for successfully obtaining these invertebrates. Table 3 presents the common names, Order and capture method of the invertebrates that capuchins eat at our study site, based on a previous study on invertebrate foraging (Young 2005) and on data collected during this study.

Behavioural data collection

Behavioural data were collected from May to August 2004 and January to May 2005, encompassing both wet and dry seasons. Each of the two monkey groups was followed for two consecutive days a week, from dawn until dusk. We

Table 3 Details of invertebrates eaten by white-faced capuchins in Santa Rosa National Park

Common name	Order	Capture category
Dead head cockroach	Blattodea	Large extracted
Grasshoppers	Orthoptera	Surface-dwelling and large extracted
Katydid	Orthoptera	Surface-dwelling
Stink bugs	Hemiptera	Surface-dwelling
Cicadas	Hemiptera	Surface-dwelling
Beetles	Coleoptera	Surface-dwelling
Stick Insect	Phasmida	Surface-dwelling
Scorpions	Scorpiones	Large extracted
Spiders	Araneae	Large extracted
Ants	Hymenoptera	Small extracted
Wasps	Hymenoptera	Small extracted
Termites	Isoptera	Small extracted
Unknown	Unknown	Surface-dwelling, small extracted and large extracted

used focal animal sampling (Altmann 1974) and chose focal individuals semi-randomly, using a schedule that rotated through age-sex classes. To the best of our ability, we collected equal data on each individual. If the focal monkey was out of sight for longer than 10% of the total sampling period, the sample was discarded. We collected a total of 246 h of data. During feeding bouts, we recorded the type of food and, where appropriate, species, ripeness, color and stage of maturity. For the purposes of this study “foraging” behaviours encompass visual foraging, extractive foraging, feeding and food handling.

Data analysis

We evaluated potential niche divergence in foraging patterns between dichromatic and trichromatic monkeys by decomposing foraging activity into a nested set of four independent components:

1. Proportion of the total observed time spent in foraging behaviours.
2. Proportion of total foraging time spent on fruit foraging (vs insect foraging).
3. Proportion of total fruit foraging time devoted to foraging on cryptic fruit (as opposed to conspicuous fruit).
4. Proportion of total insect foraging time devoted to surface-dwelling insects (as opposed to imbedded insects).

By choosing a nested set of components and by rescaling each component of foraging as a proportion, these four

components are independent of each other in the sense that high values of one component do not presuppose that there must be high (or low) values in another component. All proportions were arcsine square root transformed, as the analysis of these kinds of proportion data are appropriately dealt with by transformation followed by parametric analysis (Crawley 2005).

We used a multi-way ANOVA procedure in SPSS 14.0 to test for effects of color vision phenotype on our foraging variables. We also included analyses for four other predictor variables: age, dominance rank, social group and sex. Given the sex-linked nature of polymorphic color vision and the opsin homogeneity of the CP study group (Hiramatsu et al. 2005; Jack and Fedigan 2007), if the effects of group, dominance, sex, and visual phenotype were to be analysed directly there would be a serious confounding of effects. Instead, we tested our variables in a manner that attempts to isolate the potential effects each by using a set of planned comparisons of relevant subsets within the composite variables. This also allowed us to utilise all of the data to assess error variance while still focusing on comparisons that provided the best insights to the effects of group, dominance, sex and visual phenotype. A single value for each foraging variable was calculated for each individual monkey. All analyses in which that individual was included use the same values. We ensured that the homogeneity of variance criterion was met for each analysis.

Age

The first analysis we ran was to test for a main effect of age by comparing adults to juveniles for our four foraging variables. We excluded juveniles from subsequent analyses if significant differences were present.

Dominance

To test for the effects of dominance, we compared dominant females with subordinate females, leaving out the males entirely and also females of intermediate dominance. We therefore tested the main effect of a composite dominance/sex variable. We chose females for this analysis, because female dominance is predicted to be linked to foraging pressures (Trivers 1972) and to avoid confounding the test for dominance with a sex effect. In the planned comparison, we included only the two highest ranking and the two lowest ranking females in each group, to avoid issues concerning linearity of dominance hierarchies in these groups. This test is the most sensitive to differences between high and low ranking individuals. Fortunately, an equal distribution of color vision phenotypes (two dichromats and two trichromats in each dominance group) was present in this subset.

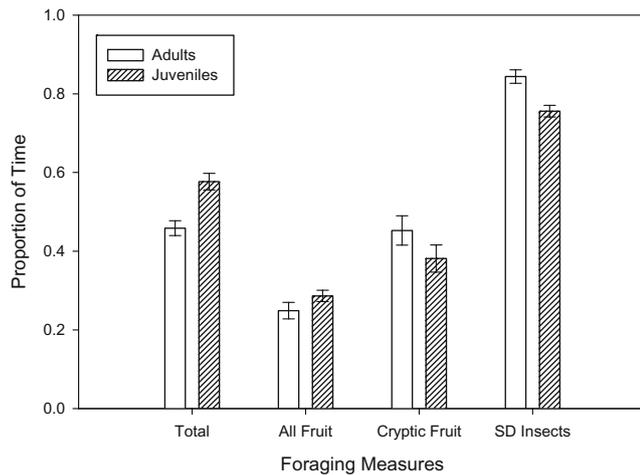


Fig. 1 Foraging time budgets of adult and juvenile white-faced capuchins for different food types: overall time spent foraging; foraging time spent on fruit; fruit foraging time spent on cryptic fruit; insect foraging time spent on surface-dwelling (SD) insects. Data are presented as mean proportion of time \pm standard error, back-transformed from arcsine square root values

Social group

We evaluated an effect of social group membership we ran an ANOVA testing the main effect of a composite social group/sex variable. Specifically, we compared the males between the CP and LV group. This avoided confounding effects of sex and color vision phenotype, because females are excluded and all males are dichromats. Dominance is unlikely to confound the results because each group has a range of dominance ranks.

Sex and color vision phenotype

To evaluate the final two predictor variables, we ran two planned comparisons within an ANOVA wherein individuals were grouped into one of three categories according to their sex and phenotype: (1) male dichromat; (2) female dichromat; (3) female trichromat. To test for the effects of sex we conducted a planned comparison between female dichromats and male dichromats as part of the partitioning of the overall phenotype/sex effect. This removed the potentially confounding effects of visual phenotype. To test for the effects of visual phenotype we conducted a planned comparison of trichromatic females to dichromatic females thereby avoiding the potential confounding effect of sex.

Results

Age

We first tested whether juveniles ($N=14$) and adults ($N=19$) differed for any of the four variables (Fig. 1). We found that

juveniles spent a significantly larger proportion of their time foraging than adults did ($F_{1,31}=17.03$, $p<0.001$). We also found that juveniles spent significantly less time foraging on surface-dwelling insects as a proportion of foraging time spent on all insects ($F_{1,31}=11.86$, $p=0.002$). Juveniles and adults did not differ in time spent foraging on fruits overall ($F_{1,31}=1.85$, $p=0.18$) or in time spent foraging on cryptic fruit within total fruit foraging time ($F_{1,31}=1.85$, $p=0.18$). However, the differences found in the other two measures indicate that the foraging time budget of juveniles and adults does differ in at least two important respects, so therefore we only considered adults for the remaining analyses.

Rank

We compared the two most dominant females in each group to the two least dominant females in each group ($N=8$) as a contrast within an overall ANOVA that included all adults ($N=19$). We found that high ranking individuals were not significantly different from low ranking individuals for any of the four foraging variables (Fig. 2): Overall time spent foraging ($t_{16}=0.33$, $p=0.74$); foraging time spent on fruit ($t_{16}=-0.45$, $p=0.66$); fruit foraging time spent on cryptic fruit ($t_{16}=-0.24$, $p=0.81$); insect foraging time spent on surface-dwelling insects ($t_{16}=0.66$, $p=0.52$).

Social group

We compared the individuals in the CP study group to those in the LV study group (Fig. 3). To run this test, while controlling for the sex and color vision of the group members, we compared LV males ($N=5$) to CP males ($N=3$) as a contrast

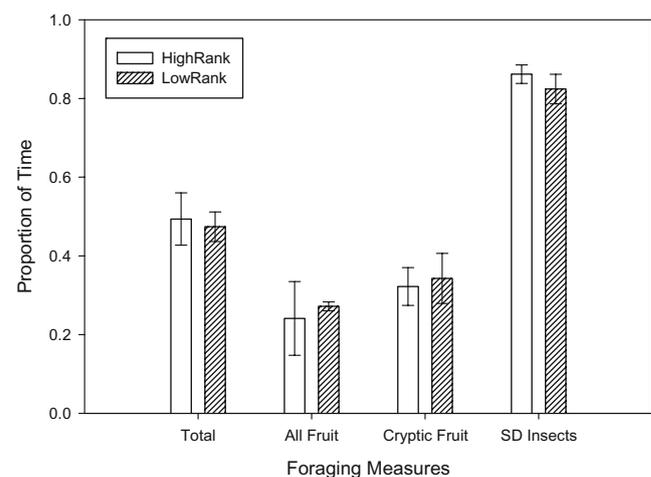


Fig. 2 Foraging time budgets of high and low ranking adult female white-faced capuchins for different food types: overall time spent foraging; foraging time spent on fruit; fruit foraging time spent on cryptic fruit; insect foraging time spent on surface-dwelling (SD) insects. Data are presented as mean proportion of time \pm standard error, back-transformed from arcsine square root values

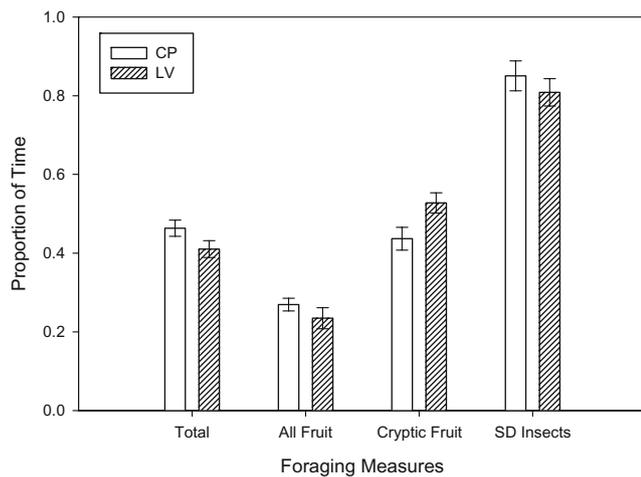


Fig. 3 Foraging time budgets of adult male white-faced capuchins in two study groups, CP and LV, for different food types: overall time spent foraging; foraging time spent on fruit; fruit foraging time spent on cryptic fruit; insect foraging time spent on surface-dwelling (SD) insects. Data are presented as mean proportion of time \pm standard error, back-transformed from arcsine square root values

within the overall ANOVA of all adults ($N=19$). No significant differences were found between the two study groups for overall time spent foraging ($t_{15}=-1.47$, $p=0.16$), foraging time spent on fruit ($t_{15}=-0.52$, $p=0.61$), fruit foraging time spent on cryptic fruit ($t_{15}=0.73$, $p=0.48$), or insect foraging time on surface-dwelling insects ($t_{15}=-0.72$, $p=0.48$).

Sex and color vision

In our final analysis, we ran two contrasts where all adults ($N=19$) were grouped according to their color vision and sex into one of three groups: (dichromatic) males ($N=8$), dichromatic females ($N=5$) or trichromatic females ($N=6$). The mean values for each of these three groups are presented in Fig. 4. We found dichromatic females spent significantly more time foraging overall than males did ($t_{16}=4.62$, $p<0.001$). No significant difference existed between males and females for any of the three remaining foraging variables tested: foraging time spent on fruit ($t_{16}=-0.89$, $p=0.38$); fruit foraging time spent on cryptic fruit ($t_{16}=-0.77$, $p=0.46$); insect foraging time on surface-dwelling insects ($t_{15}=-0.016$, $p=0.99$).

Our second contrast compared dichromatic females to trichromatic females to test for an effect of color vision phenotype independent of sex. Dichromatic females spent more time overall foraging than trichromatic females did ($t_{16}=5.07$, $p<0.001$). Dichromats and trichromats did not differ in foraging time spent on fruit ($t_{16}=-1.63$, $p=0.12$), fruit foraging time spent on cryptic fruit ($t_{16}=-0.046$, $p=0.96$), nor insect foraging time on surface-dwelling insects ($t_{15}=-1.31$, $p=0.21$).

Discussion

Understanding niche divergence in capuchin foraging patterns

Intra-specific foraging niche divergence in primates is not a new idea. Capuchin monkeys can be very dispersed (Fragaszy et al. 2004) during feeding and other foraging behaviours, which account for approximately 50% of the mean capuchin activity budget (McCabe 2005). The capuchin diet is highly variable (Fragaszy et al. 2004; McCabe 2005) and at any given point in time members of a group will be exploiting different resources, including fruit, flowers, small embedded insects, surface-dwelling insects, vertebrate prey (Melin and Fedigan, unpublished data). The degree of group cohesiveness in primates varies intra- and inter-specifically and is affected by the interplay of variables such as group size and demographic composition, ecological variables, such as resource availability and abundance, and predation and infanticide risk (Wrangham 1980; Hausfater and Hrdy 1984; Hill and Lee 1998; Boinski and Garber 2000). Differences in foraging budget, diets or feeding rates of individuals within the same group based on age, sex class, reproductive condition or dominance have been noted in the current study and others (Rose 1994; Vogel 2004; McCabe 2005). Previous studies have also found that monkeys will forage in different areas of the forest, use different support structures, take up different positions within the group (central vs peripheral; forward vs back) and that these are affected by dominance, age and sex (Weckman, Melin and Fedigan, unpublished data, Fragaszy et al. 2004; Rose 1994). While it is well

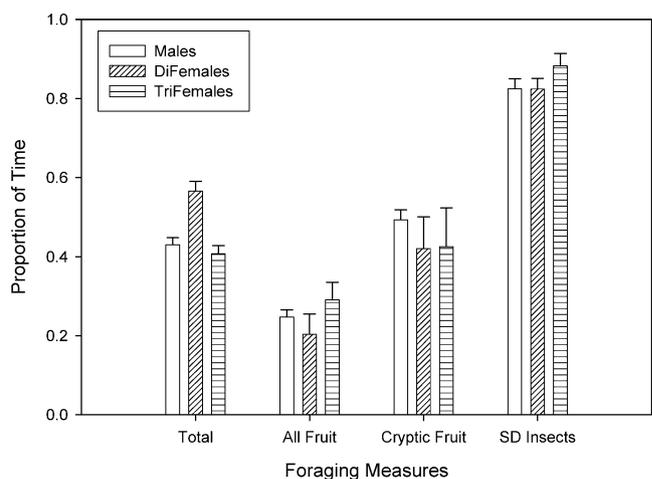


Fig. 4 Foraging time budgets of adult male, dichromatic female and trichromatic female white-faced capuchins for different food types: overall time spent foraging; foraging time spent on fruit; fruit foraging time spent on cryptic fruit; insect foraging time spent on surface-dwelling (SD) insects. Data are presented as mean proportion of time \pm standard error, back-transformed from arcsine square root values

understood that group living confines the behaviours of individuals and their foraging options (Chapman and Chapman 2000; Strier 2000), it is clear that the potential for some degree of niche divergence is present within a group of foraging monkeys. Color vision phenotype has also been suggested to play a role in foraging niche divergence among monkeys (Mollon et al. 1984). We evaluated this hypothesis for the first time in our current study.

The role of color vision phenotype in niche divergence

Monkeys with different color vision phenotypes may be differentially suited for the foraging tasks with which they are faced (Jacobs 1997; Regan et al. 2001; Caine et al. 2003). Based on this line of reasoning, it has been suggested that trichromatic and dichromatic monkeys may specialise on different resources (Mollon et al. 1984; Jacobs 1997). This type of niche divergence in diet and foraging budget can reduce intra-group competition for resources and therefore potentially increase individual fitness of all group members. In this study, we evaluated whether foraging niche divergence occurs between monkeys of different phenotypes by examining whether dichromatic and trichromatic capuchins differentially allocated their foraging time budget to different types of resources.

Our results do not support the hypothesis that foraging niche divergence is involved in maintaining polymorphic color vision in our study population, at least insofar as the variables we evaluated are considered. Dichromatic and trichromatic monkeys did not differ in the amount of foraging time they devoted to fruit foraging vs insect foraging. Nor did they differ from each other in the amount of time they devoted to foraging on conspicuously colored vs cryptic fruit. We also did not detect a significant difference between phenotypes in the amount of insect foraging time individuals devoted to surface-dwelling insects, which we argue are cryptic resources, vs imbedded insects that rely on mechanical protection afforded by substrates as their primary defense mechanism.

Our predictions of niche divergence between dichromats and trichromats were based on the assumption that individuals are differentially advantaged for obtaining certain types of food resources based on their color vision phenotype. Specifically, that trichromats are better suited at detecting or selecting conspicuous ripe fruit (Osorio and Vorobyev 1996; Sumner and Mollon 2000b; Sumner and Mollon 2000a), which translates to increased feeding efficiency for these resources over dichromats. Experimental studies using naturalistic food items support this suggestion (Caine and Mundy 2000; Smith et al. 2003). The second part of the assumption is that dichromats are better at breaking camouflage (Morgan et al. 1992; Saito et al. 2005b), which facilitates higher capture rates of surface-dwelling insects (Melin et al. 2007) and increased feeding

rates on cryptic fruits (Caine et al. 2003) by dichromats than trichromats. The lack of niche divergence we observed could be explained in that other factors such as nutritional requirements, sex, or food availability are stronger predictors of foraging choices than color vision phenotype is.

However, it is also possible that the differences in foraging efficiency and energy intake rates between dichromats and trichromats seen in studies on captive primates do not exist for wild primates. A recent study on white-faced capuchins found no differences in the feeding rates of dichromatic and trichromatic capuchins for several fruit species (Vogel et al. 2007). These results contrast with the argument that phenotypes differ in foraging ability. A lack of niche divergence may therefore also be explained if there are no functional differences present in the foraging efficiencies of phenotypes in free-ranging populations. Our current study was not designed to evaluate foraging efficiency, because time spent in foraging behaviours does not reflect foraging success and energy gain. Studies addressing different measures of foraging efficiency, which include measures of ingestion rates and investigation sequences, will contribute to our ongoing understanding of the role of color vision in foraging.

Other evolutionary mechanisms

What of the other three hypotheses proposed to date to explain polymorphic color vision in neotropical primates? One of our results may be consistent with the heterozygote advantage hypothesis. When we analysed the proportion of the total observed foraging time (to control for any initial variation in foraging effort by individuals in the study before we evaluated for finer differences in foraging choices), we found that dichromatic females spent more time foraging than trichromatic females did. One interpretation of this finding is that trichromats are able to obtain necessary sustenance in less time, which may translate into a fitness advantage. However, this interpretation assumes that trichromats have higher feeding rates or energy intake and a recent field study does not support this assumption (Vogel et al. 2007). While some support for the heterozygote advantage hypothesis is present (e.g., Riba-Hernandez et al. 2005; Smith et al. 2003), it is too early to discount the impact of other evolutionary mechanisms. Evidence of dichromat advantage has been put forth for polymorphic primates (Caine et al. 2003; Melin et al. 2007) and additionally evidence for heterozygote advantage in wild populations remains scanty. Continued field studies in this area are required to evaluate the possibility of a heterozygote advantage more fully.

Future directions

While investigations of polymorphic color vision in natural populations of New World primates have recently began in

earnest, in large part due to recent advances in field color quantification and genetic techniques (Lucas et al. 2001; Surridge et al. 2002), much remains to be determined. For example, the potential for other types of niche divergence among phenotypes, e.g. habitat partitioning into different forest locations based on the quality and quantity of illuminating light, has been suggested (Mollon et al. 1984; Tovee et al. 1992; Regan et al. 2001) and remains to be evaluated in detail. Factors such as time of day, weather, height in the canopy, the density of surrounding vegetation affect the quantity and quality of natural illumination (Endler 1993; Yamashita et al. 2005) and would need to be taken into consideration. Further, the interactions among the visual environment, foraging decisions and feeding efficiency of the monkeys may be important because a positive or negative effect of the illuminant for any given phenotype will depend on the nature of the detection task. For example, trichromats may be at an advantage in dim light for finding ripe fruit (Osorio et al. 2004), while dichromats may be advantaged in dim light for finding cryptic foods (Melin et al. 2007).

It is also desirable to include larger sample sizes to evaluate for differences among the several trichromat phenotypes and dichromat phenotypes, rather than just comparing trichromat to dichromats. Larger sample sizes will also make it easier to tease apart the influence of confounding variables, such as sex and group. Additionally, incorporating objective measures of the reflectance of diet items and illumination in different forest environments will make classifications of food items less subjective. Finally, future investigations incorporating comparative approaches among different species and study sites will no doubt help researchers understand the evolutionary and proximate selective pressures acting on primate color vision.

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